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A NEW SALAMANDER, GENUS *BATRACHOSEPS*,
FROM THE INYO MOUNTAINS OF CALIFORNIA,
WITH A DISCUSSION OF RELATIONSHIPS IN THE GENUS

By Ronald William Marlow, John M. Brode, and David B. Wake



The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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A NEW SALAMANDER, GENUS *BATRACHOSEPS*, FROM THE INYO MOUNTAINS OF CALIFORNIA, WITH A DISCUSSION OF RELATIONSHIPS IN THE GENUS¹

By Ronald William Marlow,² John M. Brode,³ and David B. Wake^{2,4}

ABSTRACT: A newly discovered species of plethodontid salamander from the Inyo Mountains in the northern Mojave Desert, California, is described as *Batrachoseps campi*. This new species helps bridge the gap between *Batrachoseps* and members of the tropical supergenus *Bolitoglossa*, and may well be the most generalized of all bolitoglossine salamanders. *Batrachoseps campi* and *B. aridus* are the only plethodontid salamanders known to be restricted to localized mesic microhabitats surrounded by desert. The new species is very generalized in morphology. In some respects it resembles *B. wrighti* of Oregon, but it also shares some features with *B. aridus*. On the basis of its distinctive morphology and distribution, *B. campi* is thought to be a survivor of an early stage in the evolution of the genus. The Inyo Mountains region may have served as the habitat of the species throughout much of the Tertiary. Recommendations are made for preservation of the fragile habitats in which the species lives.

In 1970 Brame described the first terrestrial salamander endemic to desert habitats. *Batrachoseps aridus* occurs in a highly restricted, mesic microhabitat in the desert of southern California. We now announce the discovery of a second species of lungless salamanders, family Plethodontidae, known from desert regions. The new species was discovered in the fall of 1973 in two canyons along the west slope of the Inyo Mountains at the northern edge of the Mojave Desert near the Owens Valley, California. This strikingly distinct form is so different from other *Batrachoseps* in its robustness and coloration that we initially thought it to be a species of *Hydromantes*, or even of a new genus. Upon further examination it proved to be a structurally generalized member of the genus *Batrachoseps*, very similar to a postulated ancestor of the entire genus and not much removed from the ancestral stock of the tribe Bolitoglossini (including *Hydromantes* and all of the neotropical plethodontid salamanders, in addition to *Batrachoseps*). Like *B. aridus*, the species seems to occur only in restricted, mesic microhabitats in a setting that is seemingly harsh and inhospitable for salamanders. Yet, the apparent absence of any populations even remotely similar to this species in areas more favorable for salamanders suggests that the Inyo Mountains have long been the home of the species. These mountains are relatively ancient, and in fact may represent remnants of the original crest of the Sierra Nevada before the modern mountains were uplifted to the west (Bateman and Wahrhaftig 1966). Possibly these salamanders have been in the Inyo Mountains throughout Cenozoic times.

The new species is named in honor of the late Charles L. Camp, herpetologist, paleontologist, and historian, who contributed greatly to our knowledge of the American West. Professor Camp discovered the genus *Hydromantes* in the New World, described *H. platycephalus*, participated in the discovery and description of *H. shastae*, and very early recognized the diversi-

fication within the genus *Batrachoseps* in his description of *B. major*. The species shall be known as:

Batrachoseps campi NEW SPECIES

Figures 1, 6, 7, 8, 11

Suggested common name: Inyo Mountains Salamander.

HOLOTYPE: MVZ 122993, an adult female from Long John Canyon, W slope of the Inyo Mountains, elevation 1695 m (5560 ft), 3.2 km (2 mi) (airline) N, 5.3 km (3.3 mi) E Lone Pine, Inyo County, California, USA; collected by John M. Brode and Ronald William Marlow on September 26, 1973.

PARATYPES: MVZ 122994–122996 (3 specimens), same data as the holotype; MVZ 123011–123015 (5 specimens), same locality as holotype, collected October 20, 1973; MVZ 122997 – 123009, 123017 – 123031 (28 specimens), LACM 122004 – 122011 (8 specimens), French Spring, W slope of the Inyo Mountains, elevation 1829 m (6000 ft), 6.4 km (4 mi) N, 5.7 km (3.6 mi) E Lone Pine, Inyo County, California.

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FIGURE 1. *Batrachoseps campi* (MVZ 123023), an adult female (40.4 SL) from Long John Canyon, Inyo Mountains, Inyo County, California. Photograph by James Hendel, Scientific Photography Laboratory, University of California, Berkeley. Scale is 25 mm.

DIAGNOSIS: A large, robust species of *Batrachoseps* (individuals identifiable to sex, 16 males: 41.3–53.3, mean 45.3 SL⁵; 23 females: 32.0–60.7, mean 45.5 SL) with a short tail, broad head and large feet; distinguished from all members of the genus by these characters and by its distinctive coloration (dark brown-black ground color with moderate to large patches of light gray iridophores on upper eyelids and irregularly spread over head and anterior part of trunk, and lacking a dorsal stripe or band that is lighter than the ground color); distinguished from *B. aridus* by its much larger size (largest known *B. aridus* are less than 40 mm SL), relatively shorter tail, and fewer vertebrae (19–20 versus 17–19); further distinguished from species which approach it in adult size by its much broader head, fewer trunk vertebrae (except *B. wrighti*) and much shorter tail. *Batrachoseps campi* is the only member of the genus that has paired prefrontal bones and divided premaxillary bones from early juvenile stages throughout adult life.

DESCRIPTION: *Batrachoseps campi* is the most generalized member of the genus in its morphology. The species is relatively large and has a large, broadly rounded snout. Nostrils are small and typical of the genus. There are no protuberances associated with the distinct nasolabial grooves. No mental hedonic glands have been observed in males. The head is very broad (SL 6.6–7.1, mean 6.8 times head width in 6 males and 6.3–7.5, mean 7.0 in females over 45 SL). Grooving patterns of head, throat and neck are typical of the genus. Eyes are relatively large and moderately protuberant. Vomerine teeth are borne in long series (mean total 16.5); frequently the teeth extend nearly to the lateral edge of the internal nares. Small maxillary teeth extend beyond the center of the eyeball; they increase in number with increasing size and are relatively numerous (mean total 46). Pre-maxillary teeth are small and numerous (8–10 in adult males; 6–17 in adult females); they are in an advanced position in the males, but barely protrude through the lip. Costal grooves between appressed limbs (counting one each in axilla and groin) range from 16–18 with a strong mode of 17. The tail is short for this genus and tapered; tail length in 20 adults over 45 SL is 0.62–0.88, mean 0.76 (± 0.06) times SL, with no discernible sexual dimorphism. The tail has no basal constriction, and is

nearly round. However, an irregular row of enlarged glands is present on the dorsal surface of the tail. These glands form pustule-like protuberances that are more lightly colored than surrounding surfaces. The postiliac gland is a small, grayish spot that is not conspicuous. Limbs are long for the genus, and leave from 2–5 intercostal folds uncovered when appressed (mean 3.66 ± 0.89 ; $n = 47$). Standard length ranges from 4.2–5.3 (mean 4.8 ± 0.3) times hind limb length in 16 females, and from 4.5–5.1 (mean 4.8 ± 0.25) in males. The hands and feet are large for this genus. Webbing is insignificant, and the four fingers and four toes are all discrete. The third digit of both manus and pes is far longer than the others. All digits have bulbous tips and large subdigital pads. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 2, 4, 1.

MEASUREMENTS (OF HOLOTYPE): Head width, 8.4; snout to gular fold (head length), 12.8; head depth at posterior angle of jaw, 2.9; eyelid length, 3.3; eyelid width, 2.0; anterior rim of orbit to snout, 1.7; horizontal orbital diameter, 1.9; inter-orbital distance, 3.8; distance between vomerine teeth and paraspheroid tooth patch, 0.2; snout to fore limb, 5.7; distance separating internal nares, 2.4; distance separating external nares, 2.6; snout projection beyond mandible, 0.9; snout to posterior angle of vent (standard length), 60.7; snout to anterior angle of vent, 56.1; axilla to groin length, 32.5; tail length, 48.5; tail width at base, 4.3; tail depth at base, 3.7; fore limb length, 11.1; hind limb length, 12.1; width of right hand, 3.4; width of right foot, 4.0.

COLORATION: This is a dark salamander that differs from all other *Batrachoseps* in lacking a dorsal stripe at all ages. The ground color is very dark brown-black in most individuals, but a lighter brown-black in some. This is the result of a dense network of melanophores, covering the whole body with few or no gaps. The only additional color is a scattering of silvery iridophores which when grouped together form patches with a slightly greenish hue. Patches of iridophores are concentrated on the upper

⁵SL = standard length, the distance from the snout to the posterior angle of the vent; all measurements in this paper are in millimeters, unless stated otherwise.



FIGURE 2. Type locality of *Batrachoseps campi*, Long John Canyon, Inyo Mountains, Inyo County, California. Camera is aimed southeast. Salamanders were found inside the mouth of the canyon, under surface objects in the shaded area.

eyelids of most individuals, and in a series of spots of varying size lying mainly on the posterior part of the head, the neck, and the dorsum in the vicinity of the insertion of the hind limbs. Elsewhere, including the nearly immaculate venter, the iridophores are scarce and small. These cells fade and disappear after a short time in alcohol. The dorsal glands of the tail are prominent near the tail base in many of the individuals. They appear to be brown-tan in color, the result of a thinning of the ground color. The iris is dark and featureless.

REMARKS: There is little sexual dimorphism in this species. Mean SL of males and females in the sample is similar, but females appear to reach larger sizes than males. Females have vertically folded vent margins, whereas males have dense, short papillae in the anterior half of the vent.

Some large females in the sample have enlarged, yellow ovarian eggs. Testes of most adult males are large and unpigmented. Vasa deferentia are heavily pigmented in most adult males. The two largest males (50.4, 53.3) have bilobed testes. The smallest male with bilobed testes is 45.0 SL, and the largest male with unilobed testes is 47.4 SL. Males 43.3 and 49.0 SL have a second lobe forming, and a male 48.6 SL has two lobes.

When uncovered, individuals of *B. campi* displayed no special defensive behavior of the kind observed in other species of the genus (Stebbins and Lowe, 1947; Brame, Long, and Chiri, 1973). Apparently immobility is the sole defensive behavior.

HABITAT: The western slopes of the Inyo Mountains receive approximately 22 cm of precipitation each year, much of it coming in snowfall. Vegetation on the slopes is sparse and stunted with extensive areas of open, rocky substrate. Long John Canyon is narrow and winding with rock walls rising almost vertically for about 150 m. At the type locality the canyon axis is east-west and the canyon floor is about 10 m wide (Fig. 2). The floor of the canyon is strewn with boulders and flood-carried rubble. A permanent spring at the type locality provides enough moisture for a dense, nearly impenetrable growth of woody shrubs (average height about 2 m) filling the canyon floor and extending approximately 100 m. This appears to be the extent of the available surface habitat, though crevices and subterranean water courses may provide extensive underground habitat.

Salamanders were found under rocks in fine, dark soil (a sandy loam) that was wet enough that a cast formed in the hand withstood taps with the finger. As many as four animals were taken under a single large rock (25 x 40 cm). This is a heavily shaded canyon. On October 20 the sun shone on the canyon bottom at 10:30, but by noon the canyon was entirely shaded.

The flora of the canyon floor is dominated by dense stands of *Salix* sp., *Forestiera neomexicana* and *Rosa Woodsii*. Also present were *Erodium* sp., *Artemisia Dracunculul*, *A. ludoviciana*, *Clematis ligusticifolia*, *Aquilegia formosa*, *Gutierrezia microcephala*, *Philadelphus microphyllus*, *Clrysanthamnus teretifolius*

Table 1. Classification matrix based on discriminant analysis of 229 specimens of nine species of *Batrachoseps*, including juveniles and adults of both sexes. Entries along the main diagonal are "correct" matches of individuals to their source populations based on twelve morphological characters.

Group	Number of Individuals Classified into Group							
	1	2	3	4	5	6	8	9
1 <i>aridus</i>	13	0	0	0	0	0	0	1
2 <i>stebbinsi</i>	0	29	1	0	0	0	0	0
3 <i>simatus</i>	0	3	23	0	2	0	0	1
4 <i>attenuatus</i>	0	0	0	27	3	0	0	0
5 <i>major</i>	0	0	1	1	26	0	0	2
6 <i>campi</i>	0	0	0	0	0	46	0	0
8 <i>wrighti</i>	1	1	0	0	0	0	18	0
9 <i>pacificus</i>	0	1	0	0	0	0	0	29

and *Haplopappus cuneatus*.

The second locality, French Spring, is 6.4 km (4 mi) (airline) north and 5.7 km (3.6 mi) (airline) east of Lone Pine, Inyo Co., California, at an elevation of about 1800 m. The water flow of this spring is much more extensive than in Long John Canyon. The flow from the spring cascades down approximately 300 m of naturally terraced rocky hillside and approximately 300 m of canyon floor, before disappearing in the sand. Vegetation is similar to that at the type locality (Fig. 3).

COMPARISONS: Both bivariate and multivariate morphometric analyses have been used to compare *B. campi* with other described species of *Batrachoseps*. For these comparisons the following juvenile and adult specimens were used (all deposited in LACM and MVZ, catalogue numbers and measurements on file at MVZ): 14 *B. aridus* (type locality); 30 *B. stebbinsi* (type series); 29 *B. simatus* (type series); 30 *B. attenuatus* (San Francisco, Calif.); 30 *B. major* (vicinity of Los Angeles, Calif.); 46 *B. campi* (type series); 20 *B. wrighti* (central Oregon); 30 *B. pacificus* (Santa Cruz Island). Only *B. relicus*, a highly variable species currently under study by Kay Yanev, was omitted. The latter species is small and slender, and is most similar in morphology to *B. attenuatus*. Data for the following characters were used: SL, head width, hind limb length, front limb length, limb interval, total maxillary teeth, total vomerine teeth, tail length, front foot width, hind foot width, head length, number of trunk vertebrae. Bivariate plots of head width, limb length and foot width against standard length were produced for comparison with the results of Brame and Murray (1968), and tooth number and tail length were also plotted against standard length. The results of the bivariate analysis indicated that most characters distinguish *B. campi* from some other species and some characters (head width, Fig. 4) distinguish *B. campi* from nearly all other *Batrachoseps* (compare with Fig. 9, Brame and Murray 1968). The species differ greatly in adult size, thus making direct comparison of individual features and even bivariate analysis difficult. However, the species of *Batrachoseps* are readily distinguished by combinations of three characters or more, and we believe multivariate discrimination is the method of choice. Canonical variate analysis was chosen to discriminate between the species. In particular, we wished to determine how distinct *B. campi* was relative to species it resembled most closely, based on bivariate analysis. The University of California, Berkeley, version of the BMD07M program for stepwise discriminate analysis was used (see Lynch and Wake 1975, for description).

The main result of the discriminate analysis is the demonstra-

tion of the distinctiveness of *B. campi* relative to other species of *Batrachoseps*. Even among the remaining species of the genus there is a moderate amount of discrimination, but we emphasize that we are not considering geographic variation here. A feature of the program used is a classification matrix which gives the number of "correct" and "incorrect" assignments of individuals to their proper populations on the basis of morphological criteria alone (see Lynch and Wake 1975). The classification matrix (Table 1) assigned all 46 specimens of *B. campi* to the correct population on morphological grounds. There are from one (*B. pacificus*, *B. aridus*, *B. wrighti*) to six (*B. simatus*) mis-classifications in the other species, but overall 92 per cent of the classifications are correct. The first three canonical variables account for 93 per cent of the observed interspecific variance. The first two canonical axes are illustrated in Figure 5.

Along the first axis (accounting for 69 per cent of the interspecific variance) species are separated mainly by factors related to size (standard length, head width). Limb interval and tail length also contribute importantly. *B. campi* is well separated from all other species. *B. aridus*, *B. stebbinsi*, *B. wrighti* and *B. pacificus* are relatively close to *B. campi* along this axis; *B. attenuatus*, *B. major*, and *B. simatus* are relatively remote.

The second axis (accounting for 16 per cent of the total interspecific variance) separates *B. wrighti* from all other species, but seems to add little to discrimination among remaining species. Based on the magnitude of standardized coefficients of the canonical variables, head width, numbers of trunk vertebrae and foot width contribute most to discrimination along this axis.

The third axis accounts for only about 8 per cent of the total interspecific variance. It allows separation of *B. stebbinsi* and *B. simatus* from all other species, with *B. aridus* being on the extreme end of the axis from *B. stebbinsi*. Other axes contribute little additional discrimination.

COMPARATIVE OSTEOLOGY: Osteological comparisons to other *Batrachoseps* are based on study of an adult female (49.4 SL) and a juvenile female (37.6 SL) of *B. campi*. These were cleared and stained using standard techniques. Radiographs of the type series and both cleared and stained specimens and radiographs of all other species of the genus were utilized.

Batrachoseps campi is similar to other species of *Batrachoseps* in some features of skull structure, but it is highly distinctive in others. The skull of *B. campi* is typical of the genus in proportions (Fig. 6). The characteristic dorsal fontanelle between the paired frontals and parietals is especially prominent. The fontanelle is proportionately of similar size in all species of *Batra-*

choseps, with a slightly smaller fontanelle in *B. wrighti* than in other species. Only *Batrachoseps* among all genera of salamanders has a fontanelle of this shape. In all *Batrachoseps* the skull is relatively short and broad; total skull width is 70 to 75 per cent of skull length, and *B. campi* falls about in the middle of the range of measurements.

The relatively short maxillary bones seen in *B. campi* are widespread in *Batrachoseps*. Characteristically the frontals are narrowed, appearing "pinched" between the orbits, and this is seen in *B. campi*. In all species the skull is lightly built and rather weakly articulated. However, *B. campi* has notably stronger and more extensive cranial articulations than other species.

Premaxillary bones of *B. campi* are separated in both juvenile and adult specimens. In most of the radiographed individuals, including juveniles, the divided premaxillaries can be seen clearly. In some individuals the appropriate region of the skull is obscure on the radiographs. Divided premaxillary bones are found elsewhere in the genus only in large adult *B. wrighti* (Bishop 1937, Stebbins and Lowe 1949, Wake 1966). Smaller *B. campi* than those available to us (28.5 SL) probably have a single premaxillary bone, the typical plethodontid situation; fused larval and juvenile premaxillaries separate at metamorphosis or early in life in the primitive plethodontid condition, but remain fused in a variety of derived conditions (Wake 1966).

In *B. pacificus*, *B. sinatus*, *B. stebbinsi*, *B. major*, *B. aridus* and some populations of *B. attenuatus* and *B. relictus*, the frontal processes of the premaxillary arise separately, then fuse for a distance before again separating near their tips. We see no evidence of such fusion in either *B. wrighti* or *B. campi*. The posterior tips of the frontal processes diverge greatly in *B. campi*, to a lesser degree in *B. wrighti* and only slightly in other species. As in all species of *Batrachoseps* the premaxillaries of males are larger and more protuberant than those of females, but sexual dimorphism is apparently less marked than in such species as *B. pacificus* and *B. major*, and probably less than in the other species as well.

The maxillary bones are not well articulated with other bones in *Batrachoseps*, but in *B. campi* the elements are relatively stouter than in any other species of the genus. The facial lobe of the maxillary in *B. campi* is relatively large, equalling the proportions in such large species as *B. pacificus*. Palatal portions of the maxillaries are very small. The large nasal bones are the dominant facial elements. They have a narrow spinous projection paralleling the frontal processes of the premaxillaries in *B. campi* and in other *Batrachoseps*, but these are especially pronounced in *B. campi*. Rather well developed septomaxillaries are present in all species of *Batrachoseps*.

Prefrontal bones have previously been reported only in *B. wrighti*, in which individuals over 45 mm body size have very tiny but discrete elements (Wake 1966). Well developed prefrontals are present in both the juvenile and adult *B. campi*, and, while the radiographs are not suitable for finding these elements in all instances, they can be seen in a number of the X-rayed specimens. The bones are about the size of the facial lobes of the maxillaries and are distinctly larger than the septomaxillaries. In contrast, the prefrontals which develop in large *B. wrighti* remain much smaller than the septomaxillaries.

Preorbital processes of the vomers are typically absent in *Batrachoseps*. In *B. campi* small processes that extend to the lateral margin of the internal nares (adult) or to the center of the nares (juvenile) are evident. These tooth-bearing processes are prominent in the radiographs. In other species of *Batrachoseps* the



FIGURE 3. French Spring, Inyo Mountains, Inyo County, California. Camera is aimed southeast. Salamanders were found under rocks along the stream course in the center of the photograph.

Table 2. Quantitative characteristics of the chromosomes of *Batrachoseps campi* based on haploid set of Figure 12.

Chromosome No.	Relative length ^a	Arm ratio ^b	Centromere index ^c
1	11.0	1.05	49
2	10.0	1.28	44
3	9.8	1.05	49
4	9.0	1.21	45
5	8.8	1.10	48
6	8.4	3.35	23
7	7.8	1.00	50
8	7.1	1.04	49
9	6.0	1.38	42
10	6.0	1.06	48
11	5.8	1.31	43
12	5.7	1.14	47
13	4.8	2.13	32

^a Length of chromosome/total length of haploid genome x 100.

^b Length of long arm/length of short arm.

^c Length of short arm x 100/length of whole chromosome.

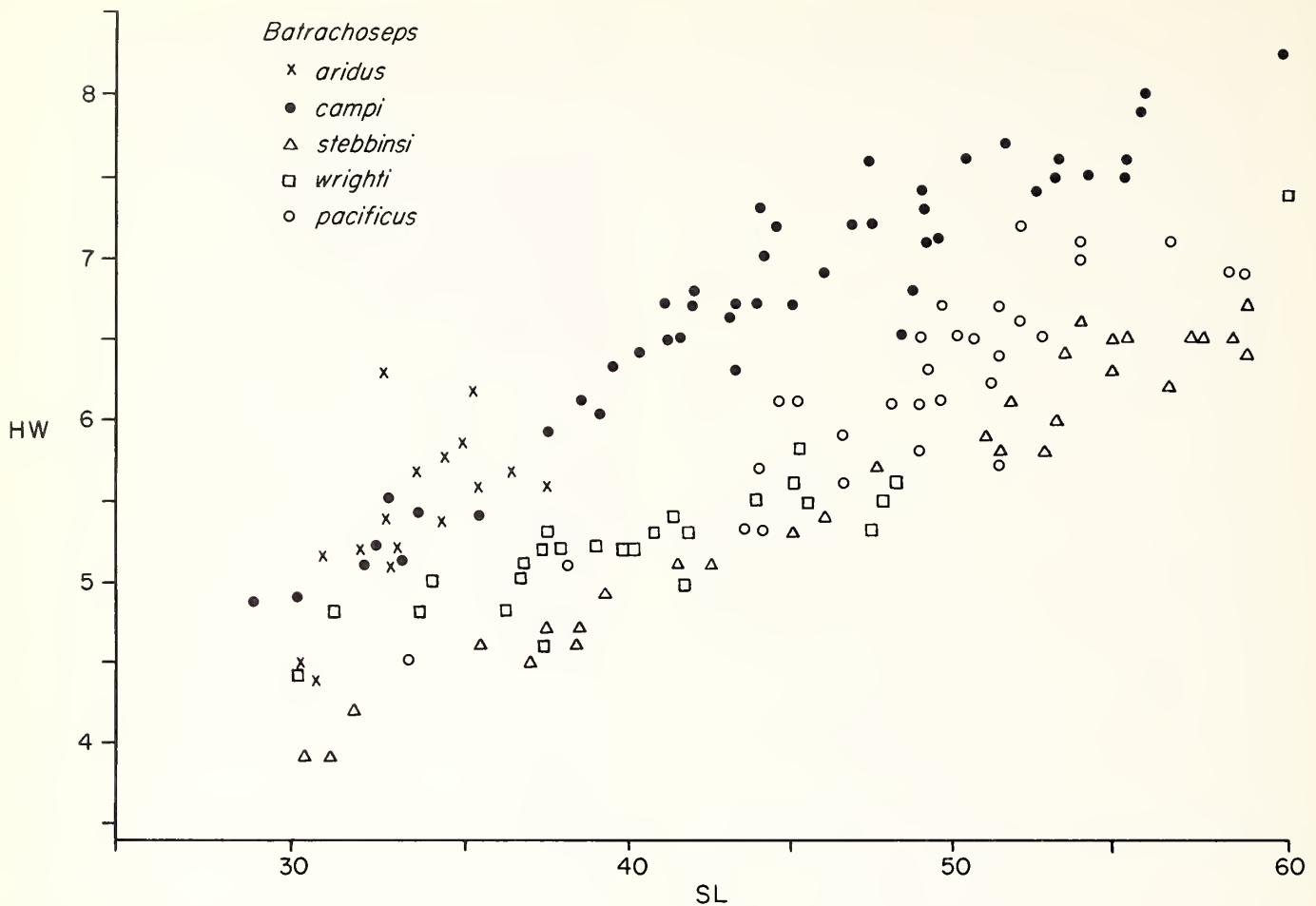


FIGURE 4. Relation of head width to standard length in the five species of *Batrachoseps* having the broadest heads in the genus.

processes are usually mere suggestions of bone growth behind the nares (Fig. 7), but there are two exceptions. In a radiograph of one very large *B. wrighti* (reported by Brame 1964) a small process is clearly evident, and very small processes are evident in a radiograph of one adult *B. aridus*.

The nasolacrimal duct extends anteroventrally from the corner of the eye to the cartilaginous nasal capsule. The opening in the nasal capsule lies in the gap between the facial process of the maxillary and the nasal. Typically, slight evaginations in the lateral margins of the nasals, or more rarely in the anterodorsal margin of the maxillary, mark the route of the duct in species of *Batrachoseps*. In *B. campi* the duct produces slight dorsal concavities in the anterior part of the prefrontals as well.

Frontal bones in *Batrachoseps* contribute importantly to the facial part of the skull, especially by means of a long attenuated process that extends anteriorly below the frontal processes of the premaxillary. In *B. campi* the facial portion of the frontal is relatively less developed than in other species and there is no spinous process. Further, only the tips of the premaxillaries overlap the frontals. In other respects, the frontals in *B. campi* are similar to those in other *Batrachoseps*, with the characteristic posterior divergence of the bones. *B. wrighti* has relatively the widest frontals. Frontals are about one-half the total skull length in *B. campi*, *B. wrighti* and *B. pacificus*, but on the order of two-thirds

the total skull length in *B. stebbinsi*, *B. aridus*, and the other species.

All species have small parietal bones, with no clear differentiation among the species in terms of relative size. The bones usually fall short of the narrow occipital bridge portion of the skull. In all species a well defined lateral spur is present on the parietal (see Wake 1966), and it is particularly stout in *B. campi*.

Squamosal and quadrate bones are small and have no special features in any single species. Dentaries are slender and similar in structure in all species. Prearticulars have low coronoid processes. All species have columellar processes extending from the opercular plate. These processes are well developed in *B. campi*.

Teeth of *Batrachoseps* typically occur on premaxillary, maxillary, dentary, and vomerine elements, and in addition there is a paired patch of teeth along the parasphenoid. The patches vary greatly within and between species in size and number of teeth.

The hyobranchial apparatus is typical of the genus *Batrachoseps* in all important respects (see Lombard and Wake 1977) including the long, recurved radii, the absence of a lingual cartilage, the basibranchial of relatively uniform width, and the relatively long epibranchial. The genioglossal muscles are slender and elongate. These muscles have a unique arrangement in *Batrachoseps*, originating from the mandible near the jaw articulation and proceeding well forward before extending to the midline

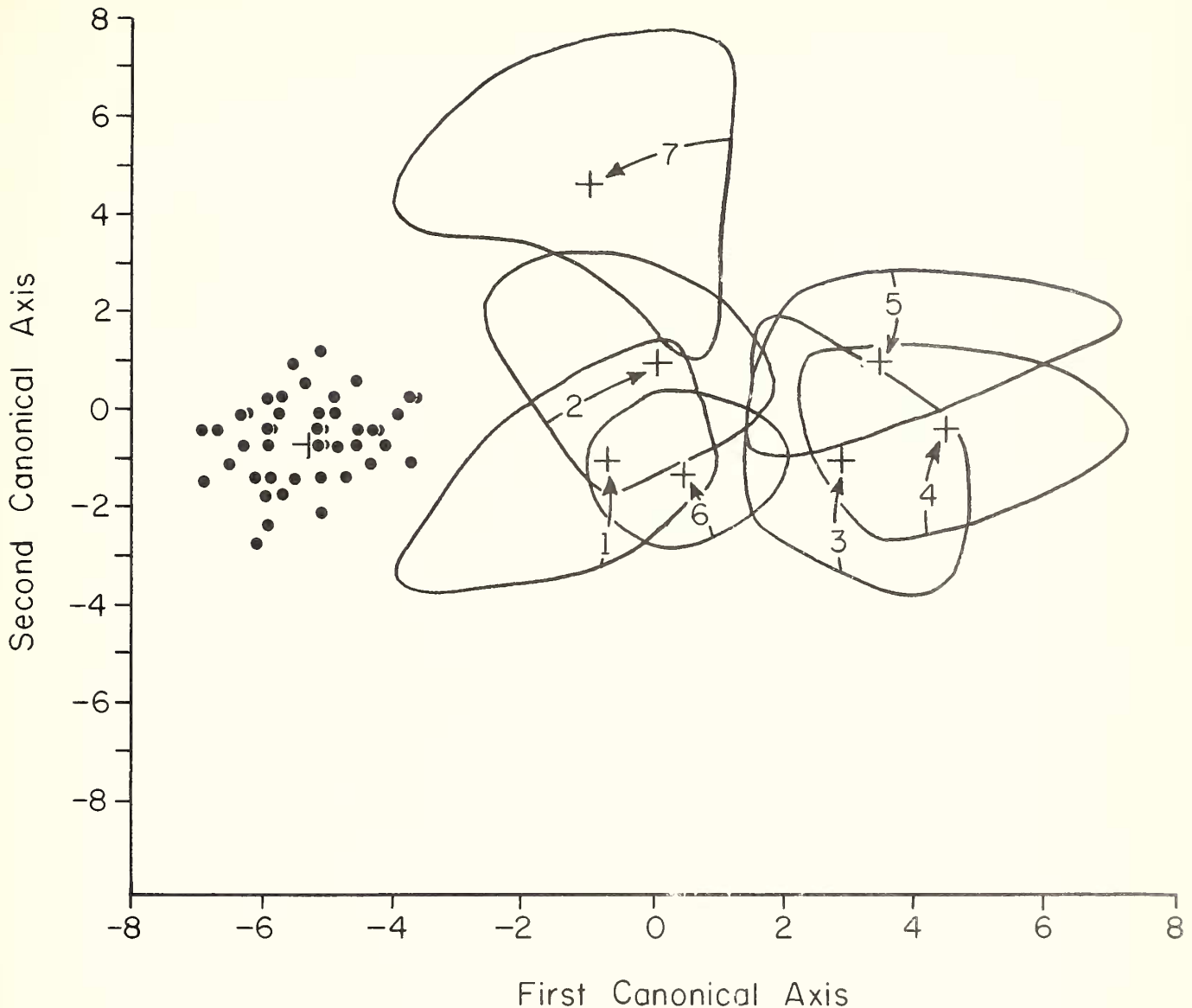


FIGURE 5. Plot of first two canonical variates for adults of eight species of *Batrachoseps*. The discriminant analysis includes 12 morphological variables. The first variate (abscissa) accounts for 69 per cent of the observed interspecific variance. The cross marks the centroid for each species. All individuals for each species are enclosed within the indicated perimeter except for *B. campi*, where all individuals are spotted. 1. *B. aridus*, 2. *B. stebbinsi*, 3. *B. simanus*, 4. *B. attenuatus*, 5. *B. major*, 6. *B. pacificus*, 7. *B. wrighti*.

and dorsally into the tongue (Piatt 1935).

Trunk vertebrae in *Batrachoseps* number from 16 to 23, but any single population has a maximal range of variation of four. *B. wrighti*, the species with the shortest trunk, has a modal number of 17. Some populations of *B. relictus* also have a modal number of 17, but others have modal numbers as high as 21. In *B. campi* there is a strong mode of 18, with a range of 17–19 (mean = $17.9 \pm .42$ SD). All individuals from Long John Canyon have 18 trunk vertebrae. *B. aridus* has a strong mode of 19, with a range of 19–20 (Brame, 1970). The remaining species all have higher numbers of trunk vertebrae, with both *B. major* and *B. attenuatus* having modes as high as 22, and occasional individuals of these species and *B. relictus* having as many as 23.

Genera of plethodontid salamanders have either two or three

caudosacral vertebrae, with the exception of *Batrachoseps*, in which both numbers may occur in a single population (Wake 1966). *B. campi* is typical of the genus, some individuals having two and others, three.

Complete tails are present in 32 of the type series of *B. campi*. In these individuals postsacral vertebrae (including either 2 or 3 caudosacral and all of the caudals) range from 22–34 (mean 28.44 ± 2.18), with numbers increasing from juveniles to adults. This is a very low number for *Batrachoseps*, but accurate comparative data are not available for other species. The main problem in obtaining accurate counts is the high frequency of tail breaks. However, numbers as high as 60 caudal vertebrae occur in some of the species. Relatively few caudal vertebrae might also be expected in the relatively short-tailed *B. aridus*, but our

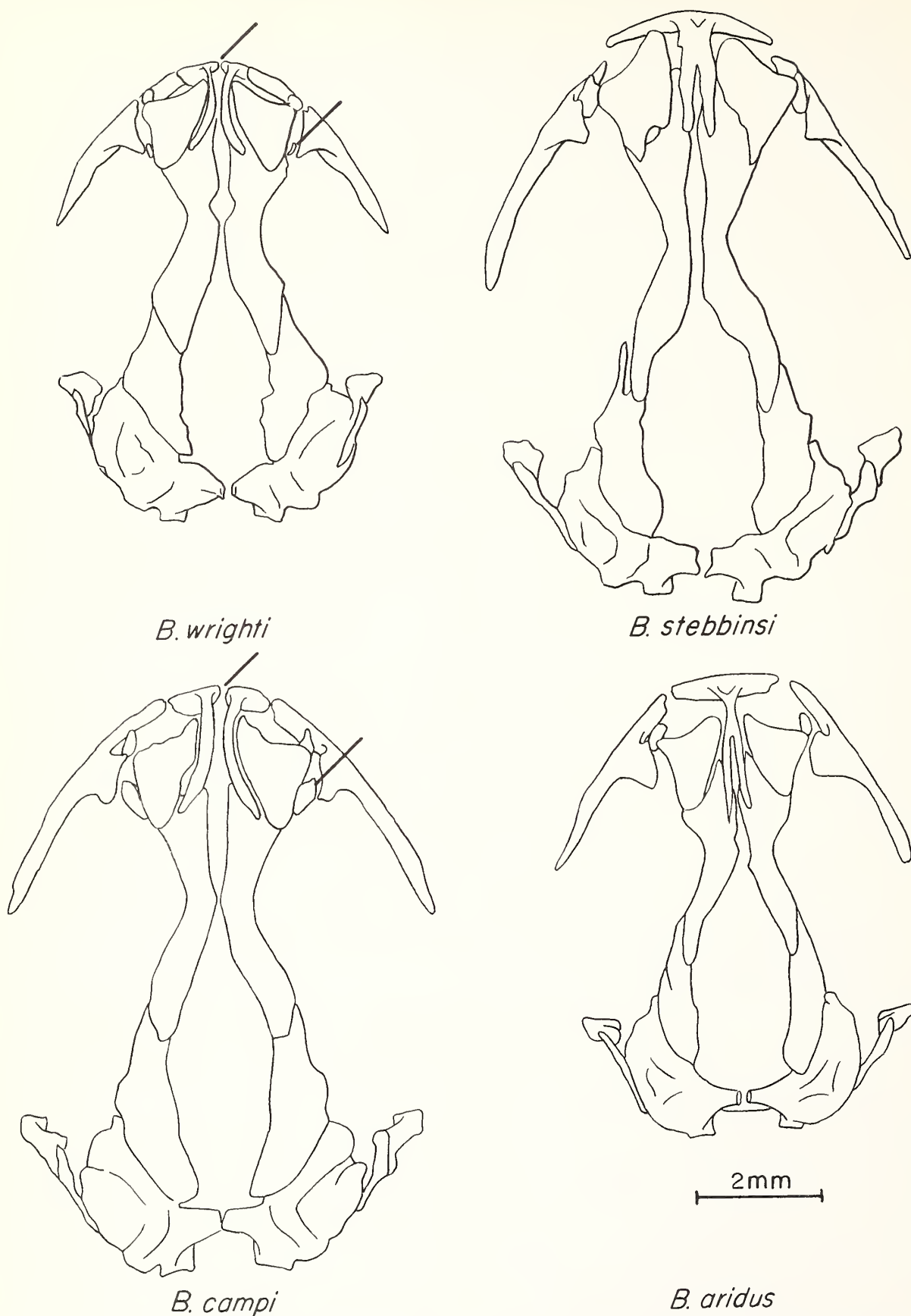


FIGURE 6. Dorsal views of the skulls of four species of *Batrachoseps*. The lines indicate the divided premaxillary bones and the prefrontal bones found only in *B. campi* and *B. wrighti*.

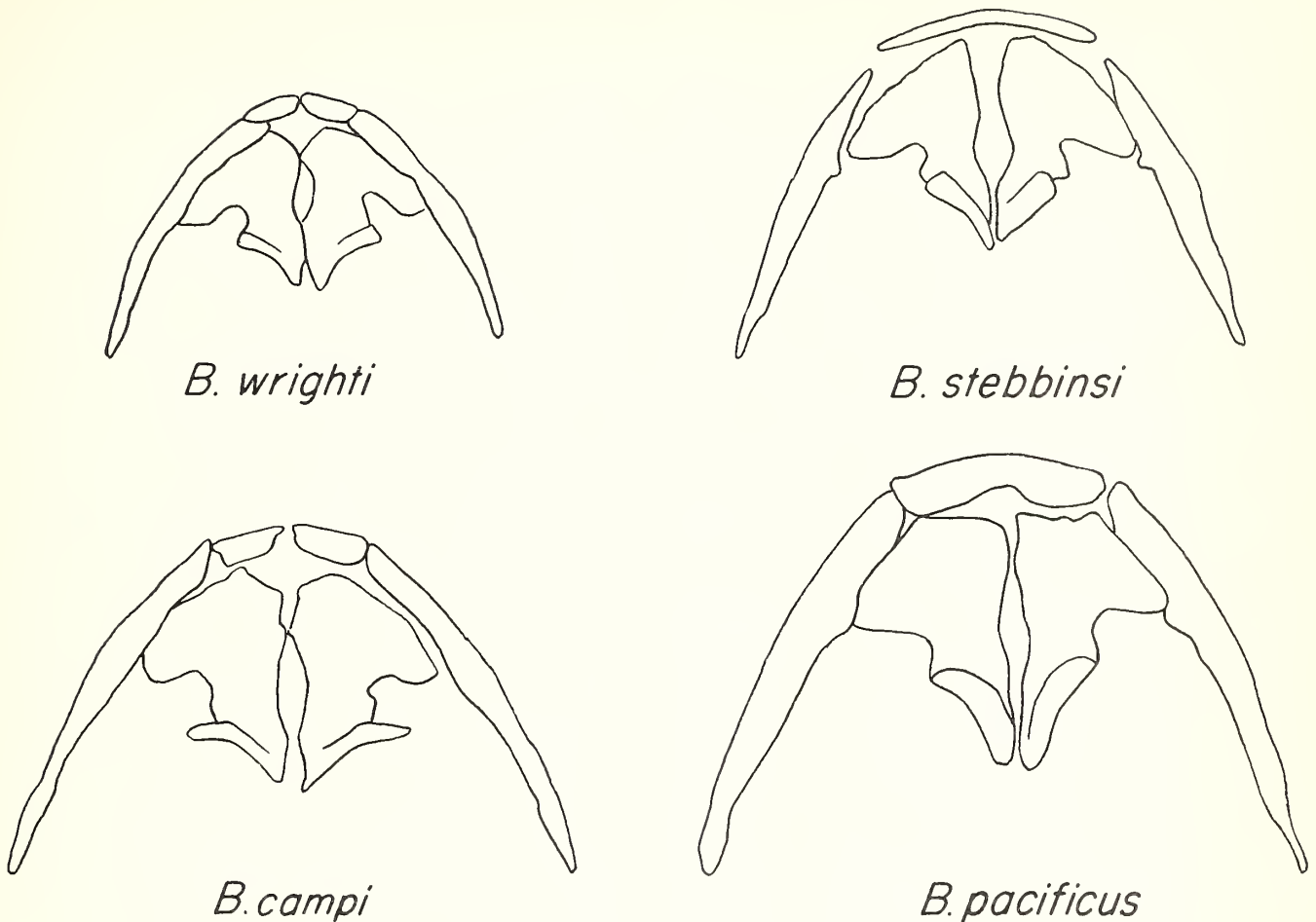


FIGURE 7. Ventral view of the anterior part of the skull of four species of *Batrachoseps*. The bones are the premaxillaries, maxillaries, and vomers. Teeth not indicated. Same scale as Figure 6.

largest cleared specimen (41.0 SL) has 32 (a total of 34 post-sacra) and larger specimens reasonably could be expected to have more. In *B. wrighti*, also relatively short-tailed, as many as 38 caudal vertebrae are present.

The limbs of *B. campi* are stouter than those of most other *Batrachoseps* but are of about the same relative length as those of *B. stebbinsi*. In osteological detail they are very similar to those of the more generalized species of *Batrachoseps* (Fig. 8). The tibial spur is well developed in *B. campi*. This structure is absent in many populations of *B. attenuatus*, but is characteristically present in other species. Wake (1966) reported that all species of *Batrachoseps* except *B. wrighti* and some populations of *B. pacificus* (these particular populations are now referred to *B. major*, following Brame and Murray 1968) have seven rather than the primitive plethodontid number of eight carpal elements as the result of fusion of the ulnare and intermedium cartilages. We have found eight carpals in some *B. major* and in most specimens of *B. wrighti*, but other members of these species have seven. All populations of *Batrachoseps* have eight tarsal elements. *B. campi* has seven carpals and eight tarsals. The usual phalangeal formula in *Batrachoseps* is 1-2-3-2 for both hand and foot, but Wake (1966) and Brame (1970) report 0-2-3-2 rarely in *B. attenuatus*. Brame and Murray (1968) and Brame (1970) also indicate that *B. stebbinsi* and *B. aridus* differ from

other species in lacking a phalanx on the first digit of the hand and foot. A small terminal phalanx is present on the first digit of the hand in four of five specimens examined of *B. aridus*, and on the first digit of the foot in two of these specimens. Extremely small phalanges that do not appear on radiographs are present on the first digit of both hands and feet in all nine specimens of cleared *B. stebbinsi* available to us. These are often only dots of mineralized tissue, and in one foot in each of two specimens no sign of a phalanx is seen. Terminal phalanges of the first digit are also greatly reduced in *B. simatus*, and in one foot of one individual (of a total of 13) this phalanx is absent. In *B. campi* the hands and feet are relatively large and stout. The generalized phalangeal formula is present. The first phalanx is well developed and discrete. Phalanges are especially well ossified with relatively little cartilage, especially in large adults (Fig. 8). Expansion of the most terminal phalanx of each digit is characteristic of all species of *Batrachoseps*, including *B. campi*.

EVOLUTIONARY RELATIONSHIPS: Those of us who discovered *B. campi* were impressed immediately with its robustness and its relatively short body and tail. We thought it might be a representative of *Hydromantes* or some other genus, and did not think of assigning the new species to *Batrachoseps* until we noticed that it had but four toes. The species is hardly a typical *Batrachoseps*, as that taxon has been understood, and its discov-

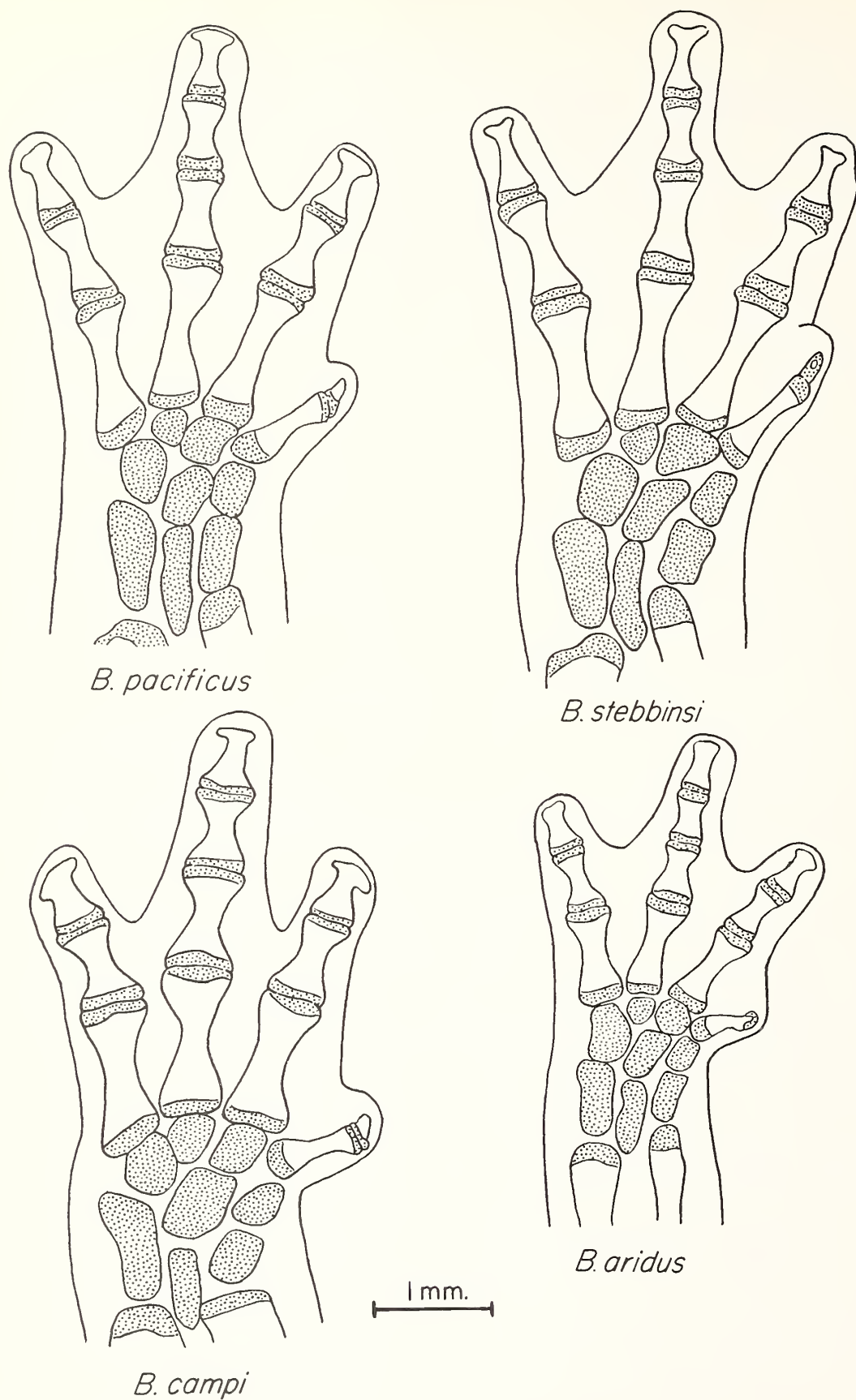


FIGURE 8. Feet of four species of *Batrachoseps*, drawn from cleared and stained specimens with aid of microprojector. Cartilage stippled.

ery forces us to re-evaluate the status of the genus.

In several morphological features *B. campi* approaches hypothesized ancestral states for the entire tribe Bolitoglossini (*Batrachoseps*, *Hydromantes*, and the tropical salamander groups in the supergenus *Bolitoglossa*—*Pseudoeurycea*, *Chiropterotriton*, *Oedipina*, *Thorius*, *Lineatriton*, *Parvimolge*, and *Bolitoglossa*). The species is more generalized than other *Batrachoseps* in osteology and myology as well as in external form. Features in which it retains ancestral conditions as compared to existing conditions in *Hydromantes* include presence of prefrontals and of genioglossal muscles. It matches *Hydromantes* in having paired premaxillaries. The paired premaxillaries distinguish it from all described species of the supergenus *Bolitoglossa*. Only the absence of a fifth toe (including tarsal, metatarsal and phalanges) and the presence of a fontanelle in the skull roof remove *B. campi* from the presumed ancestral state for the tribe Bolitoglossini (for comparative data see Wake 1966).

Perhaps *B. campi* is a very early derivative of the ancestral stock of all bolitoglossines, representing a lineage that appeared shortly after the differentiation of the *Batrachoseps* stock from a more generalized ancestral group. The superficial similarity of *B. campi* to members of such genera as *Hydromantes*, *Chiropterotriton*, and *Pseudoeurycea* may reflect the great conservatism inherent in these relatively ancient lineages. Nevertheless *B. campi* can rather easily be accommodated in the genus *Batrachoseps* so long as *B. wrighti* is also included. The close relationship of *B. campi* to other species of *Batrachoseps* rather than to other bolitoglossines is evident, based on the number and nature of derived features that are shared. It is in ancestral features that *B. campi* resembles members of other genera.

The discovery of *B. campi* and knowledge of its structure tend to make the tribe Bolitoglossini a somewhat tighter unit than formerly perceived. However, no new insight is provided into relationships of *Batrachoseps* as a unit relative to *Hydromantes* and the supergenus *Bolitoglossa*. There is no reason to modify the conclusions of Wake (1966) that *Batrachoseps* is cladistically closer to the supergenus *Bolitoglossa* than to *Hydromantes*. The single most important piece of evidence is the derived karyotype of *Batrachoseps* and the supergenus *Bolitoglossa*, both groups having a haploid chromosome number of 13 as opposed to the 14 chromosomes characteristic of *Hydromantes* and all other plethodontids (Kezer 1964; Kezer and Macgregor 1971; Morescalchi 1975).

Certain specialized and presumably derived morphological conditions are shared by *B. campi* with all other members of the genus *Batrachoseps*. Accordingly we conclude that the species is most appropriately associated with *Batrachoseps*. These features include: (1) the hyobranchial apparatus and musculature, specifically a genioglossus muscle that takes its origin near the posterior end of the mandible. This arrangement of the muscle is unique to *Batrachoseps* (Piatt 1935; Wake 1966; Lombard and Wake 1977). Further, in all other features of the apparatus the species is like other *Batrachoseps* rather than like any other genus. (2) A distinct fontanelle is present in the skull roof, bordered by markedly narrowed frontals and parietals. No comparable fontanelle is found in any other salamander. *Thorius* has a smaller fontanelle involving narrowed frontals but its parietals have proportions typical of less specialized genera.

Some derived features occur in *B. campi* and other species of *Batrachoseps* which either are less distinctive than those mentioned above, or are not exclusively present in *Batrachoseps*.

These add strength to the case for inclusion of *B. campi* in the genus. The characters include: (1) A strongly developed lateral spur on the parietal bone. This spur is shaped like that in other *Batrachoseps*, but spurs of a somewhat different shape are also present in the supergenus *Bolitoglossa* (Wake 1966). (2) The number of caudocrural vertebrae may be either two or three in a given population. Typically plethodontid species have either two or three vertebrae in this region, and only in *Batrachoseps* does intrapopulational and intraspecific variation occur (Wake 1966). (3) Four digits present on the hind foot. All other plethodontids have five digits on the hind foot, except *Hemidactylum scutatum* and *Eurycea quadridigitata*, both distinctly different from *Batrachoseps* in many features. (4) A haploid chromosome number of 13 (see Appendix).

Within the genus, *B. campi* is the most generalized species in having superficial structure similar to that of other generalized plethodontids and a number of osteological characters present in ancestral states. These latter features include notably the paired premaxillary bones, the prefrontal bones, and the preorbital processes of the vomers. Only in large, presumably old *B. wrighti* do these features appear in combination, and the first two characters are found only in *B. campi* and *B. wrighti*. All three characters are related to degree of morphogenesis (see Wake 1966, for a lengthy discussion of this issue). In plethodontids that have a larval stage, all three features are associated with metamorphosis, making their appearance at about that time. There is no metamorphosis in a technical sense in *Batrachoseps* and other salamanders with direct development, and the changes which ordinarily occur during the relatively short metamorphic period are spread out over the entire life span of these organisms. In most species of *Batrachoseps* the metamorphic features listed above are delayed in appearance to such an extent that the life span of the organism is insufficiently long for them to appear. According to this interpretation, metamorphosis of these structural features occurs early in *B. campi*, late or not at all in *B. wrighti*, and never in other species of *Batrachoseps*.

It can be argued that *B. campi* is primitive in respect to its entire pattern of development (i.e., it is the least pedomorphic), and that one should not "count" three primitive states, but only one. However one counts, *B. campi* seems to qualify as the most primitive species. In addition to its primitive osteological characters, *B. campi* has external proportions that are more similar to those of generalized plethodontids than are those of any of the other species of *Batrachoseps*. Its broad head, long limbs, relatively short trunk, and short tail are all generalized features.

It is unclear what the closest relatives of *B. campi* might be. Osteological and chromosomal comparisons suggest that *B. wrighti* is the closest relative. In addition to the features discussed above, both species have relatively low numbers of trunk vertebrae. Those features which separate *B. campi* and *B. wrighti* from other *Batrachoseps* are more striking than those which separate some other genera of salamanders within the family (Wake 1966). We considered placing *B. wrighti* and *B. campi* in the resurrected genus *Plethopsis* (Bishop 1937; see also Stebbins and Lowe 1949). However, *Plethopsis* would have to be founded on the basis of a suite of primitive characters, and given the difficulties in deciding whether we are dealing with one general metamorphic event or several independently evolving characters we believe that it is advisable to keep the genus intact. In fact, there are reasons for thinking that *B. campi* might be more closely related to some other species than *B. wrighti*. *B. aridus* is much

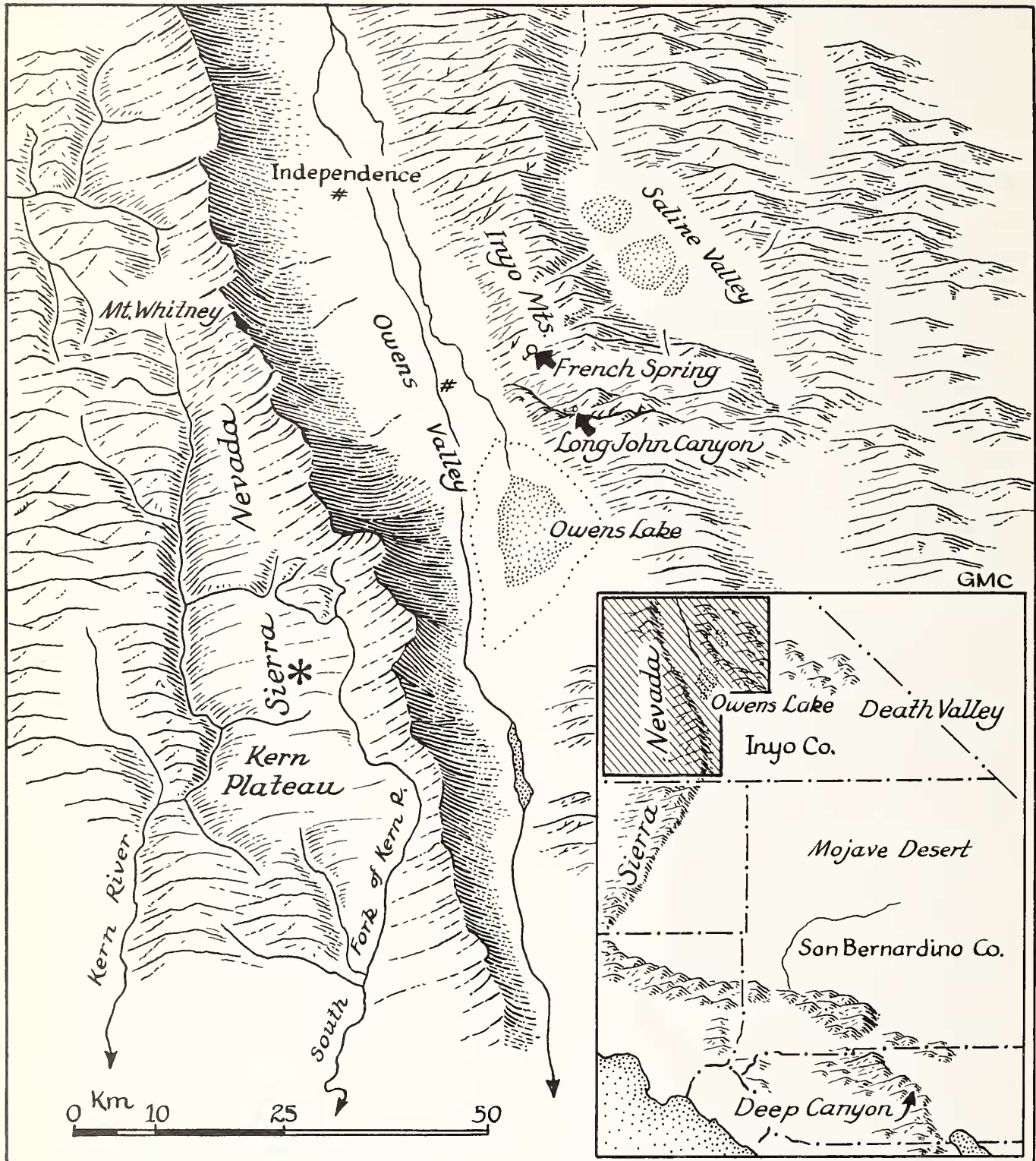


FIGURE 9. Map of eastern California showing the two localities of *Batrachoseps campi*. The closest locality for *B. stebbinsi* is indicated by an asterisk. Deep Canyon, Riverside County, California, is the only other desert locality for plethodontid salamanders (*B. aridus*) and it is indicated on the inset map.



FIGURE 10. Aerial photograph of the two localities for *Batrachoseps campi*. Note the scant vegetation. FS, French Spring; LJC, Long John Canyon. Photo courtesy of the USGS.

smaller than *B. campi*, but in many proportions it is rather similar (Fig. 4). Further, the color patterns in the two species are somewhat similar, and differ from those in all other species. Osteology provides the only certain means of separating these two species on other than size-related grounds. *B. campi* is matched in some aspects of size by *B. pacificus*, but the species are highly distinct osteologically. Further, *B. pacificus* has the characteristic striped dorsal pattern that is seen in all species except *B. aridus* and *B. campi*. Both *B. stebbinsi* and *B. pacificus* have proportions more similar to *B. campi* than any species except *B. aridus*.

The presence of *B. campi* and *B. aridus* in remote and totally isolated desert habitats raises questions concerning historical biogeography of this region. The animals survive in highly restricted microhabitats surrounded by seemingly uninhabitable desert (Figs. 9 and 10). Both species must utilize underground retreats. Possibly they can travel for some distance through crevices and solution channels in limestone formations. Brame (1970) reports limestone at the type locality of *B. aridus*. While limestone outcrops are not obvious in the two localities of *B. campi*, in parts of the southern Inyo Mountains near these localities fossil-bearing marine shales and limestones of Triassic age are found in sections up to 1,800 ft (about 550 m) thick. These rocks are exposed in many sites now and presumably they have been for long periods in the past (Oakshott 1971). The desert species of *Batrachoseps* are unlikely to be Pleistocene relics, stranded in areas of favorable habitat which they reached during pluvial stages. More likely, these species have been occupying habitats associated with exposures of these ancient rocks for a long period, perhaps since early Tertiary times. They may have maintained themselves in favorable microhabitats through many cycles of heating and cooling, moistening and drying. Had they entered desert habitats during Pleistocene pluvial periods, they would have dispersed from somewhere. There are no extant populations in California that could have served as ancestors for either *B. aridus* or *B. campi*, and it seems unlikely that these ancestors all would have become extinct or given rise to such species as *B. stebbinsi* in the relatively short time since even the beginning of Pleistocene.

Finally we note that salamanders recently have been collected in a number of canyons in parts of the Inyo Mountains other than those mentioned here. These populations are under intense study currently.

PROTECTIVE MEASURES

Long John Canyon and French Spring are within the boundaries of National Resource Lands administered by the Bureau of Land Management. Vehicle travel in the area currently is permitted only on roads and trails established prior to November 1, 1973. Both springs are Public Water Reserves. Water cannot be appropriated, and no camping is allowed within 150 m of the water.

Better protection for these populations would be afforded if Long John Canyon in the area of the spring were closed to vehicles, and the habitat areas in both Long John Canyon and French Spring were withdrawn from potential mining. Due to its small range and limited habitat, *B. campi* qualifies as "rare" and should be afforded protection under state law.

Feral horses and burros have caused massive destruction to the vegetation and soils surrounding desert springs and water courses in the Southwest. Burros are established in the Inyo Mountains and the United States Fish and Wildlife Service and the Califor-

nia Resources Agency should assess their impact and take steps to reduce or eliminate damage. Those springs in the area where horses and burros presently occur should be carefully surveyed for other populations of salamanders.

The California Resources Agency and other agencies should re-evaluate the practice of opening and clearing desert springs, often with explosives, for the enhancement of habitat for upland game and other animals. The manipulation of fragile desert seep, spring, and stream communities for any reason should proceed only after rigorous investigation of the consequences of the anticipated activities.

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APPENDIX

Chromosomes of *Batrachoseps campi*

James Kezer has studied the chromosomes of a single *B. campi* and has graciously provided the following information which he has encouraged us to present as part of the description of this species. For some years Prof. Kezer has been accumulating information concerning the chromosomes of members of the genus *Batrachoseps*, and comparative data derive from this work.

Chromosomes of *B. campi* were obtained from the testes of an adult male. The testes were fixed in three parts absolute ethanol and one part glacial acetic acid. Testes were squashed in 45 per cent acetic acid and spermatocytes were examined for chromosomes. Unstained slides were photographed using phase-contrast optics. Data were derived from anaphase cells of the second meiotic division. Two haploid sets of chromosomes from one such cell (Fig. 11) were the source of quantitative data (Table 2) used to construct an ideogram (Fig. 12).

The haploid chromosome number of *B. campi* is 13. This is the same number found in other species of *Batrachoseps* and in the tropical salamanders of the supergenus *Bolitoglossa* (Kezer and Macgregor 1971; León and Kezer 1978). All other plethodontids that have been examined, including the remaining bolitoglossine genus *Hydromantes*, have a haploid number of 14 chromosomes.

The karyotype of *B. campi* has two chromosomes having centromeres in subterminal regions (numbers 6 and 13, Fig. 12). In *B. attenuatus* and *B. major* centromeres are all in median and submedian regions, but *B. wrighti* has two chromosomes with

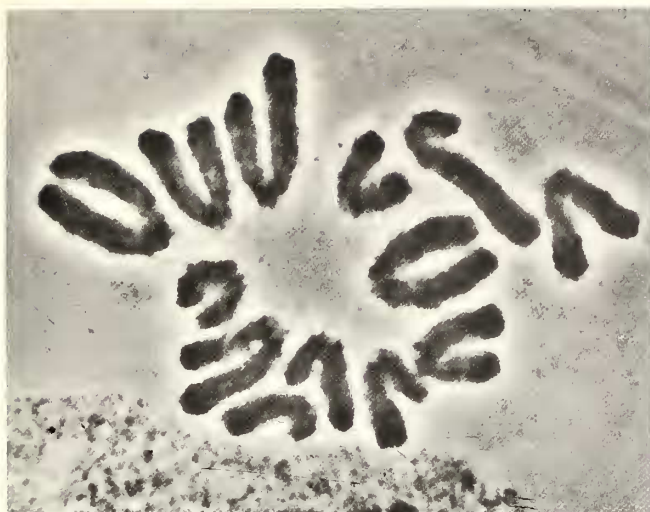


FIGURE 11. Late anaphase II chromosome preparation of *Batrachoseps campi*, prepared and photographed by James Kezer. Unstained squash. The chromosomes of this photomicrograph were used in preparing Table 2 and Figure 12.

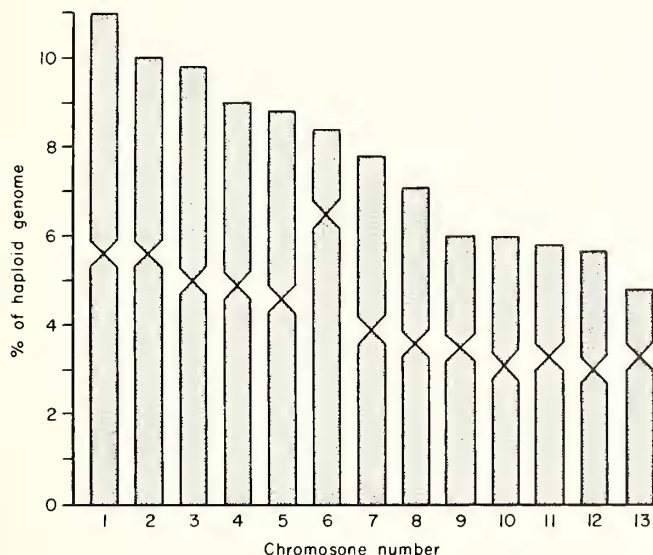


FIGURE 12. Ideogram of haploid chromosome set of *Batrachoseps campi* based on data in Table 2.

subterminal centromeres (see Kezer 1964, Fig. 7A.16). Information is not available for other species of *Batrachoseps*. At present not enough information is available to determine homologies of salamander chromosomes. Should the two subterminal chromosomes of *B. campi* prove to be homologous with those of *B. wrighti*, and should they represent derived conditions, the hypothesized close relationship of the two species would gain additional support.

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